X-RAY EFFECTS ON SEX OF PROGENY IN SCIARA COPROPHILA

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Sciara coprophila characteristically gives "unisexual" progenies; *i.e.*, the offspring from any pair mating are practically all of the same sex, either males or females. This "sex of progeny" is determined by the sex chromosome constitution of the female (Moses and Metz, 1928). Genetically there are two kinds of sex chromosomes, designated X and X′ (prime). Females are either XX or XX′; the former are male-producers, the latter female-producers (Metz and Moses, 1928). Sciara males all have the same sex chromosome constitution, form only one type of sperm, and ordinarily exert no influence on the sex ratio of their progeny. The irradiation studies presented here reveal the conditions under which the male *can* influence the sex ratio of his progeny, and thereby they clarify the relationship between "sex of progeny" and the determination of sex of the individual.

All Sciara zygotes begin development with the same chromosome complement. This complement ordinarily includes three sex chromosomes, two of which are identical sister halves of the X derived from the sperm; the third one is an X or X′ derived from the egg. At the seventh or eighth cleavage an elimination of sex chromosomes occurs in the somatic nuclei: in the production of female embryos one paternally-derived X is eliminated, in the production of male embryos both are eliminated; thus the female somatic complement comes to include two sex chromosomes, the male somatic complement only one. In the embryonic germ line the three sex chromosomes are retained until after the germ cells have migrated to the definitive gonad site; then, in both sexes alike, a paternal X is eliminated, leaving two sex chromosomes in the differentiated germ line. This pattern of sex chromosome behavior indicates that sex of the individual fly is not determined prior to chromosome elimination.

The strain of flies used in the experiments reported here produced an exceedingly low number of exceptional males (males among the progeny of female-producers) and exceptional females (females among the progeny of male-producers); progeny counts on one hundred normal females bred to normal males yielded only 0.1% exceptional sex types. A number of conditions are known which may increase the percentage of exceptional sexes. An analysis of these cases (Metz and Schmuck, 1931; Reynolds, 1938; Crouse, 1960) shows the following to be most likely: (1) that the XX-X′ mechanism controls not the sex of the progeny *per se* but rather the type of chromosome elimination which takes place in the embryonic somatic nuclei at the seventh or eighth cleavage; (2) that sex of the individual fly is governed by the somatic complement; and (3) that sex differentiation follows the pattern set by the somatic complement even when the germ line contains an irregular number of sex chromosomes.

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In the experimental studies cited above (Reynolds, 1938; Crouse, 1960) cases of nondisjunction of sex chromosomes in the female germ line were analyzed: when the zygote received two sex chromosomes from the egg, the type of chromosome elimination in the embryonic soma was strictly in accordance with the XX-XX′ mechanism. That is to say, the exceptional sex types arose *not* because of errors in chromosome elimination but rather in accordance with the sex chromosome complement remaining in the embryonic soma after elimination.

The data presented below demonstrate that irradiation can influence the transmission of sex chromosomes through the male germ line and also through the female germ line, thereby giving rise to exceptional sex types.

Material and Results

Some of the data were obtained during the course of study of x-ray-induced sex-linked recessive lethals. Females heterozygous for the sex-linked markers Wavy (X′) and swollen (X) were bred to irradiated wild type males. Wavy and swollen are not alleles but they show practically no crossing-over (see Crouse, 1943). Among the progeny there occurred a number of exceptional sons in addition to the expected daughters. The data are presented in Table I. Thus, at dosages of 2000 r, 3000 r, and 4000 r exceptional sons were induced at the frequencies of 3.9%, 9.1%, and 7.2%, respectively. Moreover, all the exceptional males were matroclinous (swollen) for their sex-linked genes; none was patroclinous. These data are interpreted as follows: as a result of the irradiation, one sex chromosome instead of two was transmitted to the zygote through the sperm; then, following the elimination of this paternal X from the embryonic soma—as directed by the mother's genotype (XX′)—only one sex chromosome (maternal) remained and the embryo differentiated into a male.

Table I

Exceptional sons derived from W′(sw) females bred to irradiated wild type males

Experiment	Dose	No. F_1 cultures	No. F_1 females	No. exc. + males	No. exc. sw males	% exc. sw males
M3X2	2000 r	9	337	0	14	$\frac{14}{351} = 3.9$
M3X3	3000 r	17	327	0	33	$\frac{33}{360} = 9.1$
M3X4	4000 r	22	593	0	46	$\frac{46}{639} = 7.2$

To establish with greater certainty that the exceptional males recorded in Table I arose not through x-ray-induced errors in chromosome elimination during embryogeny but rather through irregular sex chromosome transmission through the sperm, wild type males were x-rayed at 4000 r and bred to male-producing females. The following results were obtained: twelve F_1 cultures yielded a total of 234 sons and no exceptional daughters. Thus, the irradiation did not alter the kind of chromosome elimination determined by the XX constitution of the mother.

Another x-ray experiment was performed, this time on females, with a view

to determining whether irradiation could induce irregular sex chromosome transmission through the female germ line. Newly-emerged female-producing females (oöcytes in first meiotic prophase) heterozygous for Wavy (XX′) were irradiated at 4000 r and bred singly to swollen males. Normally such matings should yield families of daughters. Instead, the progeny derived from 26 matings included 991 females, 18 exceptional swollen (patroclinous) males, zero exceptional wild type (matroclinous) males. Clearly, nondisjunction of sex chromosomes was induced by the irradiation; the patroclinous sons were derived from embryos which received no sex chromosome from the egg and which underwent the type of somatic chromosome elimination called for by the mother's genotype (XX′); thereby they became XO in constitution and consequently differentiated into males. It is interesting to note that differentiation into a male can proceed normally in Sciara under the influence of a paternal X chromosome.

Discussion

The data presented here support the view argued previously (Crouse, 1960), that the exceptional sex types which arise in unisexual families are not the result of errors in chromosome elimination in the embryonic soma; instead they arise from irregular sex chromosome transmission through the male or through the female germ line. Sex of the individual fly is controlled by the somatic complement which obtains following elimination. This point of view, of course, does not explain the condition observed in some species of Sciara where both bisexual and unisexual families occur regularly, and where individual strains exhibiting one or the other condition are interfertile (see Metz, 1938).

Summary

Among the progeny of female-producers bred to irradiated males there appear an appreciable number of exceptional sons, all of which are matroclinous for their sex-linked genes. Among the progeny of male-producers bred to irradiated males, no exceptional daughters occur. Finally, when female-producers are irradiated and bred to stock males, exceptional sons appear in the progeny and all of them are patroclinous for their sex-linked genes. These observations, taken collectively, are interpreted as follows: irradiation of sperm or of oöcytes can result in the transmission to the zygote of an irregular number of sex chromosomes; if, following elimination, a viable somatic complement (XX or XO) obtains, the embryo will differentiate accordingly into female or male.

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